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Thermoregulation and metabolic acclimation in the Natal mole-rat (*Cryptomys hottentotus natalensis*) (Rodentia: Bathyergidae)

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Abstract

The social Natal mole-rat *Cryptomys hottentotus natalensis* has a mean (± S.D.) resting metabolic rate (RMR) when newly captured of 1.03 ± 0.25 cm^3 O_2 g^{-1} h^{-1} (n = 7) at an ambient temperature (Ta) of 30 °C, within the thermoneutral zone (TNZ) of 30–31.5 °C. Two months after maintenance in the laboratory at 26 °C, the RMR of the same animals showed a concomitant drop in value of 20 % at 30 °C (TNZ) to a mean of 0.80 ± 0.12 cm^3 O_2 g^{-1} h^{-1} (n = 14), indicating that laboratory acclimation had occurred.

The body temperature of the mole-rat is low 33.4 ± 0.83 (n = 36) and remains stable at Ta's from 10–30 °C. Above 31.5 °C, Tb increases albeit slightly to 35.7 ± 0.51 °C (n = 24). The conductance is high 0.13 ± 0.03 cm^3 O_2 g^{-1} h^{-1} $°C^{-1}$ (n = 24) at the lower limit of thermoneutrality. The mean RMR at 18 °C (the lowest Ta tested) was 1.83 ± 0.46 cm^3 O_2 g^{-1} h^{-1}, which is 2.2 times that of the RMR in the TNZ.

The nest (where mole-rats rest for up to 80 % of the day) is the focal point of the burrow system. The selection for *C. h. natalensis* to acclimate within its TNZ may relate to seasonal fluctuations in the temperature occurring in the shallow nest, resulting in seasonal acclimatisation in RMR.

Introduction

The Natal mole-rat (*Cryptomys hottentotus natalensis*) is a semi-social subterranean rodent occurring in pairs or small family groups comprising as many as six individuals (Hickman 1982). A reproductive division of labour similar to that of other species and subspecies of the genus occurs (Bennett 1988; Bennett and Jarvis 1988; Bennett 1989, 1990). In each burrow system only one female will reproduce.

The Natal mole-rat excavates extensive tunnel systems which can exceed 340 m in total length (Hickman 1979). The burrow systems are sealed from the surface and consist of numerous shallow long sub-surface foraging tunnels approximately 20 cm deep and a deeper (approximately 30 cm) central nest area slightly more protected from predators and temperature extremes (Hickman 1979; Bennett et al. 1988). *Cryptomys h. natalensis* rarely ventures onto the surface and therefore lives in a buffered thermal environment.

The systematics of the genus *Cryptomys* has been in a taxonomic disarray. Karyotypic differences in morphology involving pericentric inversions and allozyme fixations are evident between *C. h. natalensis* and *C. h. hottentotus* (Nevo et al. 1986, 1987). Indeed, Nevo et al. (1987) have suggested that the two subspecies deserve specific recognition. The size of the colonies are markedly different, with *C. h. hottentotus* occurring in colonies of up to 17 individuals (Rosenthal et al. 1992). This paper reports the RMR, TNZ, conductance and the ability to acclimate in the Natal mole-rat and compares the physiological similarities of *C. h. natalensis* with that of another species and subspecies of the genus *Cryptomys*.

Material and methods

Experimental animals

Seven *Cryptomys h. natalensis* (3 females and four males) were collected from Loteni, Natal (29° 32′ E, 29° 13′ S), Garden Castle, Natal (29° 16′ E, 29° 46′ S) and the Botanic Gardens, Durban, Natal (31° 0′ E, 29° 50′ S) in the Natal Province, South Africa. Body mass (M) of the individuals ranged from 60–182 g ($\bar{x}$ = 102, n = 7). The mole-rats were housed separately in plastic containers in a constant temperature room at 26 °C. Wood shavings and paper towelling were provided as nesting material. The mole-rats were fed on a variety of vegetables, supplemented weekly with a high protein Pronutro® cereal.

Experimental procedure

Air flow-rate was determined using a bubble flowmeter constructed of a modified burette containing soap water. The respirometer consisted of a cylindrical transparent Perspex chamber (800 cm^3) fitted with 6 mm diameter inlet and outlet ports. Temperatures were kept constant within the respirometer by placing it inside a small (0.11 m^3) temperature-controlled cabinet. A negative pressure flow-through system was used. Outside air was pulled through the respirometer, scrubbers (CO_2 trap of soda lime and water trap of colour-indicator silica gel) and oxygen analyser at a flow rate of 315–326 $cm^3\ min^{-1}$.

The techniques of Bartholomew et al. (1985) and Lighton (1985) were used to measure $\dot{V}O_2$ with an Applied Electrochemistry S-3A two-channel oxygen analyser connected to a British Broadcasting Corporation microcomputer. This procedure records the voltage between the fractional concentrations of oxygen in the respiratory and calibration streams (Lovegrove 1987). $\dot{V}O_2$ expressed as a mass-specific rate was calculated according to the equation of Depocas and Hart (1957) as:

$$\dot{V}O_2 = \frac{(F_1O_2 - F_2O_2)\ V_2}{(1 - F_1O_2)}$$

where F_1O_2, is the O_2 fraction of the inlet ir and F_2O_2 the outlet air once the chamber was connected to the measuring circuit. $\dot{V}O_2$ is expressed as $cm^3\ O_2\ g^{-1}\ h^{-1}$ and $\dot{V}_2$ is in cm^3 of air h^{-1}. Values were corrected to S.T.P. conditions.

The progress of each run was visually monitored on a visual display unit, and markers were placed on the trace to correspond with behavioural observations of resting made during the run. Each run was programmed to last 180 min, with data points being collected every 17 sec. The initial 30 min of the run was used to allow the animals to settle and consequently this section of the trace was not analysed.

A portion of the trace of approximately 20 min in length corresponding to the lowest stable oxygen consumption when the mole-rat was calm and completely at rest was integrated and calculated in $cm^3\ O_2\ g^{-1}\ h^{-1}$ (S.T.P.) and presented as the mean ± S.D. for each respective Ta. However, at lower temperatures (18 and 21 °C) portions of trace of approximately 5–10 min in length were used because the mole-rats were reluctant to rest for longer periods of time.

The relationship of $\dot{V}O_2$ and Ta, when Ta was below the lower limit of thermoneutrality (T1) was analysed using a regression analysis for repeated measures (Sokal and Rohlf 1980). Conductance below T1 was calculated from individual measurements of $\dot{V}O_2$ using the formula $Cm = \dot{V}O_2/(Tb\text{-}Ta)$ (McNab 1980) and presented as a mean ± S.D. in $cm^3\ O_2\ g^{-1}\ h^{-1}$.

Experiments were run between 08.00 h and 18.00 h to lessen the effect of any potential endogenous rhythms of metabolism. The animals were deprived of food 3 h prior to the measurement of metabolic rate in order to achieve a post-absorptive state and reduce the influence of specific dynamic action. Body (rectal) temperature (Tb) and ambient temperatures (Ta) were measured using copper-constantan thermocouples (4 mm diameter). For the rectal temperature measurements, the copper-constantan thermocouple was inserted 1.3 cm into the animal's rectum after the mole-rat had been left for 2 h at the required Ta in the temperature-controlled cabinet. To avoid undue stress at the upper and lower extremes of temperature, the mole-rats were only left in the cabinet for 1 h. Oxygen consumption was not measured below 18 °C, because the mole-rats invariably rested for too short a time period to get a meaningful $\dot{V}O_2$.

Results

The body temperature of *C. h. natalensis* remained stable at Ta's from 10 to 30 °C with a mean value of 33.4 ± 0.83 °C (n = 36). Above 31.5 °C (31.5–37 °C) Tb increased to 35.7 ± 0.51 °C (n = 34) (Fig. 1).

The mean RMR of newly captured *C. h. natalensis* was 1.03 ± 0.25 $cm^3\ O_2\ g^{-1}\ h^{-1}$

(n = 7) at 30 °C within the TNZ of 30–31.5 °C. Two months after maintenance in the laboratory at 26 °C, the RMR of the same animals showed a concomitant drop in value by 20 % at 30 °C (TNZ) to 0.80 ± 0.12 cm^3 O_2 g^{-1} h^{-1}, indicating that laboratory acclimation had resulted (Fig. 2). Below the lower limit of thermoneutrality the increase in metabolic rate is given by the equation $y = 3.582 - 0.100X$ $r^2 = 0.98$ (model for more than one value

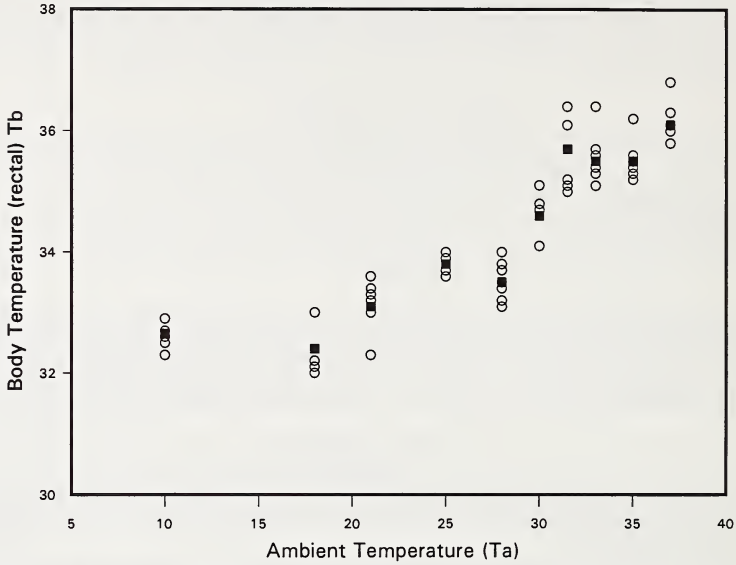

Fig. 1. Mean ■ and individual ○ body temperature (Tb) of seven Natal mole-rats, *Cryptomys hottentotus natalensis*, as a function of ambient temperature (Ta)

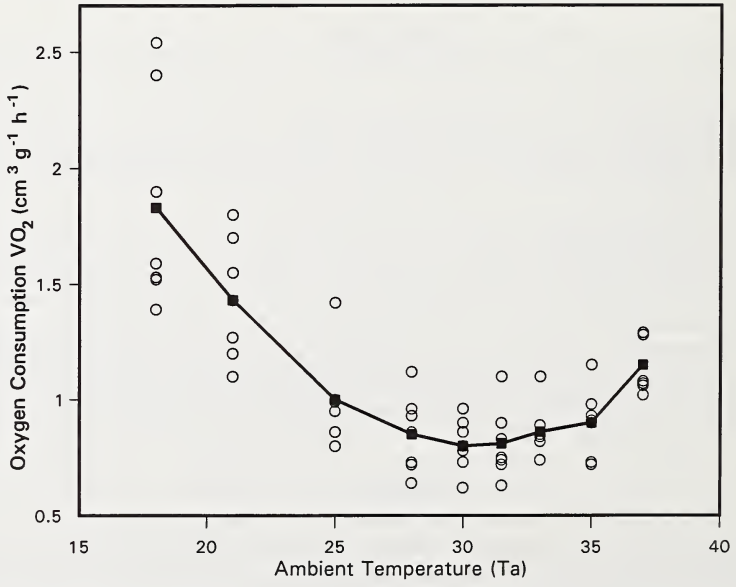

Fig. 2. Mean ■ and individual ○ oxygen consumption (cm^3 O_2 g^{-1} h^{-1}) of seven Natal mole-rats, *Cryptomys hottentotus natalensis*, as a function of ambient temperature (°C)

of y per value of x) (Sokal and Rohlf 1980). The conductance was high 0.13 ± 0.03 cm^3 O_2 g^{-1} h^{-1} (n = 24) at the lower limit of thermoneutrality. The conductance of a Natal mole-rat of mean body mass 102 g assuming a RQ of 0.8 is 73.7 mW/°C.

The mean metabolic rate at 18 °C (the lowest Ta tested) was 1.83 ± 0.46 cm^3 O_2 g^{-1} h^{-1}, which is 2.2 times that of the RMR in the TNZ. The mole-rat was able to maintain its Tb below thermoneutrality showing that the increase in heat production was sufficient to offset the greater heat loss induced by lower ambient temperature.

Discussion

Subterranean rodents spend their lives underground in sealed tunnel-systems and rarely, if ever, come to the surface (Nevo 1979). Morphological and physiological specialisations of the mole-rat permit efficient excavation, foraging and locomotion in an underground labyrinth (Eloff 1958; Lovegrove 1987; Jarvis and Bennett 1990, 1991). Foraging galleries are shallow (ca 20 cm below ground) and the temperatures experienced in these burrows represent the extremes to which the animals are exposed in the natural environment.

The annual amplitude in temperature fluctuation is greatest at the soil surface, diminishing with increasing depth. Mean annual soil temperatures vary minimally at depths exceeding 0.6 m (Bennett et al. 1988). The mole-rats spend between 70–80 % of the 24 h day resting or sleeping in the nest (Bennett 1990), and temperatures experienced in this locality will greatly influence their daily energy expenditure (D.E.E.). The nest of *C. h. natalensis* is shallow ± 20–30 cm (Hickman 1979). The shallow nest of *C. h. natalensis* probably experiences a seasonal change in core temperature.

Physiologically, subterranean rodents show traits such as low body temperatures, low resting metabolic rates and high conductances (McNab 1979). The study animal exhibited physiological adaptations characteristic of subterranean bathyergids

Mean body mass, resting metabolic rate, body temperature and social status of bathyergid subterranean rodents

Species	Mean body mass (g)	RMR cm^3 g^{-1} h^{-1}	Body temperature in TNZ (°C)	Social status	Habitat (degree of rainfall)	References
Heterocephalus glaber	39.5	0.64–1.00	32	social	semi-arid/arid	McNab (1979), Buffenstein and Yahav (1991)
Cryptomys h. darlingi	60	0.98	33	social	semi-arid	Bennett et al. (1992)
Cryptomys h. bottentotus (N. Cape)	75	0.9–1.3	34	social	semi-arid	Bennett et al. (1992)
Heliophobius argenteocinereus	88	0.85	35	solitary	mesic	McNab (1979)
Cryptomys h. bottentotus (Transvaal)	95	0.68	35.8	social	mesic	Haim and Fairall (1986)
Cryptomys h. natalensis	102	0.80–1.0	33.8	social	mesic	This study
Cryptomys damarensis	125	0.57–0.66	35	social	semi-arid/arid	Lovegrove (1986a), Bennett et al. (1992)
Georychus capensis	181	0.59	36.4	solitary	mesic	Lovegrove (1987)
Bathyergus janetta	406	0.53	34.8	solitary	semi-arid/arid	Lovegrove (1986b)
Bathyergus suillus	620	0.49	35	solitary	mesic	Lovegrove (1986b)

except that *C. h. natalensis* had a higher RMR than most of the solitary species of bathyergid rodent (Table). In contrast to previous reports on RMR's in bathyergids (Lovegrove 1986a, b, 1987) *C. h. natalensis* has a markedly higher RMR, most reminiscent of the RMRs recorded for the spalacids, geomyids (Nevo and Shkolnik 1974; Bradley et al. 1974) and the other social bathyergids (Table) (Bennett et al. 1992; Buffenstein and Yahav 1991).

Our work has shown that *C. h. natalensis* maintained in captivity (two months after capture) had a mean RMR (0.80 cm^3 O_2 g^{-1} h^{-1}) 20 % lower than when freshly (1.03 cm^3 O_2 g^{-1} h^{-1}) caught. Another subspecies of the genus *Cryptomys, C. h. hottentotus* similarly showed laboratory acclimation (Bennett et al. 1992). The nest of *C. h. hottentotus* is of comparable depth (approximately 40 cm) and again probably experiences seasonal temperature changes. In contrast, the Damaraland mole-rat, *Cryptomys damarensis* does not show metabolic acclimation to laboratory conditions. This may be the direct result of the depth of the nest, which in this species is between 1.6–2.3 m in depth (Bennett 1988).

A mole-rat utilizing a deep nest (where core temperature remains stable throughout the year) would thus have negligible selective pressures acting upon them to acclimate or seasonally acclimatise. The converse is true of dwellers of shallow nests, where there is seasonal fluctuation in nest core temperature and hence a selection to respond to these changes by adjusting the RMR. Afrotropical mole-rats occupying ecotopes which experience more equiable thermal regimes may respond in a different manner to laboratory acclimation. To date, mole-rats occurring in temperate climates with shallow nests appear to acclimate within the TNZ.

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Zusammenfassung

Thermoregulation und metabolische Anpassung beim Hottentotten-Graumull (Cryptomys hottentotus natalensis) (Rodentia: Bathyergidae)

Frischfänge der sozial lebenden Graumulle haben innerhalb ihrer thermischen Neutralzone (TNZ) von 30–31,5 °C eine mittlere Ruhestoffwechselrate (RMR) von 1,03 ± 0,25 cm^3 O_2 g^{-1} h^{-1} (n = 7). Nach zwei Monaten Haltung im Labor (26 °C) fällt die RMR der gleichen Tiere um 20 % und erreicht einen mittleren Wert von 0,80 ± 0,12 cm^3 O_2 g^{-1} h^{-1} (n = 14). Dies zeigt, daß eine Anpassung an die Laborbedingungen erfolgt ist.

Die Körpertemperatur des Graumulls ist niedrig und beträgt im Mittel 33,4 ± 0,83 °C (n = 36); sie bleibt bei Umgebungstemperaturen von 10–30 °C stabil. Über 35 °C steigt sie auf 35,7 ± 0,51 °C an (n = 24). Die Wärmeleitfähigkeit (conductance) ist an der unteren Grenze der TNZ hoch (0,13 ± 0,03 cm^3 O_2 g^{-1} h^{-1} $°C^{-1}$; n = 24). Bei 18 °C (niedrigste getestete Temperatur) beträgt die mittlere RMR 1,83 ± 0,46 cm^3 O_2 g^{-1} h^{-1}; sie liegt damit 2,2mal höher als im Bereich der TNZ.

Das Nest, in dem sich Graumulle bis zu 80 % des Tages aufhalten, ist der Mittelpunkt des Höhlensystems. Die charakteristischen Eigenschaften und die Veränderungen des Nestmikroklimas (von der Tiefe abhängig) könnten wichtige Faktoren bei der Temperaturanpassung und der jahreszeitlichen Akklimatisation sein. Die Anpassung der RMR innerhalb der TNZ steht möglicherweise im Zusammenhang mit den Temperaturschwankungen in dem nahe der Oberfläche gelegenen Nest.

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